Monitoring beak movements with an acceleration datalogger: a useful technique for assessing the feeding and breathing behaviors of sea turtles

AUTHOR(S):

Okuyama, J; Kawabata, Y; Naito, Y; Arai, N; Kobayashi, M

CITATION:

Okuyama, J ...[et al]. Monitoring beak movements with an acceleration datalogger: a useful technique for assessing the feeding and breathing behaviors of sea turtles. Endangered Species Research 2010, 10: 39-45

ISSUE DATE:

2010-03-03

URL:

http://hdl.handle.net/2433/128853

Title of manuscript

Monitoring beak movements with an acceleration datalogger can reveal the feeding and breathing behaviors of sea turtles

Running head: Monitoring feeding and breathing of turtles

Authors' names and affiliations

Junichi OKUYAMA[a], Yuuki KAWABATA[a], Yasuhiko NAITO[bc], Nobuaki ARAI[a], Masato KOBAYASHI[d]

Junichi OKUYAMA[a]

[a]Graduate School of Informatics, Kyoto University, Yoshida Honmachi, Sakyo, Kyoto, 606-8501, Japan

E-mail: okuyama@bre.soc.i.kyoto-u.ac.jp

Yuuki KAWABATA[a]

[a]Graduate School of Informatics, Kyoto University, Yoshida Honmachi, Sakyo, Kyoto, 606-8501, Japan

E-mail: yuki-k@bre.soc.i.kyoto-u.ac.jp

Yasuhiko NAITO[bc]

[b]National Institute of Polar Research, Itabashi, Tokyo, 173-8515, Japan

E-mail: yashiko@dream.ocn.ne.jp

[c]Bio-logging Institute, 2-3-10 Rex Yushima 301, Bunkyo, Tokyo, 113-0034, Japan

E-mail: bls@saturn.dti.ne.jp

Nobuaki ARAI[a]

[a]Graduate School of Informatics, Kyoto University, Yoshida Honmachi, Sakyo, Kyoto, 606-8501, Japan

E-mail: arai@i.kyoto-u.ac.jp

Masato KOBAYASHI[d]

[d]Yaeyama Station of the Stock Enhancement Technology Development Center, Seikai National Fisheries Research Institute, Fisheries Research Agency, Fukaiohta 148, Ishigaki, Okinawa 907-0451, Japan

E-mail:masakoba@affrc.go.jp

Corresponding author

Junichi OKUYAMA

Affiliation and postal address: Graduate School of Informatics, Kyoto University, Yoshida Honmachi, Sakyo, Kyoto, 606-8501, Japan

E-mail: okuyama@bre.soc.i.kyoto-u.ac.jp

Tel: +81-75-753-3296

FAX: +81-75-753-3133

Abstract:

This study was performed to determine whether the attachment of acceleration dataloggers to the lower beaks of loggerhead turtles (*Caretta caretta*) could be a useful technique for monitoring their feeding and breathing behaviors. Attaching acceleration dataloggers to the lower beak of turtles allows determination of the pitch of the head from the low frequency component of the acceleration data, and of the dynamic movements, such as biting, from the high frequency component. In addition, to determine whether the acceleration datalogger could distinguish between different food sources and feeding locations based on acceleration characteristics, we fed the turtles different types of food (squid rings, fins, and heads, including arms and tentacles) across different locations. Our results demonstrate that the acceleration datalogger was able to detect the lower beak movements of loggerhead turtles, which enabled detection of 99.6 ± 1.1 % of feeding and 100 % of breathing behaviors, with false detection rates of 24.8 ± 12.4 % and 2.4 %, respectively. In addition, our results demonstrate that it is possible to determine whether feeding on the prey requires a strong biting force, and to differentiate between feeding on the sea floor and feeding in the water column. Attaching an acceleration datalogger is a useful technique for monitoring the feeding and breathing behaviors of sea turtles. Future studies employing acceleration dataloggers should provide new insights into the biology of sea turtles and their feeding and diving strategies.

68 Keyword: Bio-logging, *Caretta caretta*, Feeding ecology, Respiratory physiology

69

INTRODUCTION

Advances in microelectronics in recent years have allowed researchers to develop small, lightweight dataloggers to minimize their physiological and hydrodynamic impacts on animals (Hawkins 2004, Naito 2004). Consequently, researchers can now attach dataloggers to wild animals to study the behavior, physiology and ecology of species that are difficult to observe (Ropert-Coudert & Wilson 2005). Animal-borne "bio-logging" technology is increasingly being applied to the study of animal biology and conservation (Cooke et al. 2004, Ropert-Coudert & Wilson 2005, Wilson et al. 2008).

The miniaturization of dataloggers with a variety of sensing abilities has enabled researchers to monitor the movements of isolated body parts of animals such as the beak or mandible (Wilson et al. 2002) and flipper (Hays et al. 2004). One of the most recent techniques is the recording of the beak-opening events of an animal by using an IMASEN (Inter-MAnibular Angle SENsor; Wilson et al. 2002) with a magnet/Hall sensor combination connected to a datalogger that records changes in the inter-mandible angle. This technique is a useful tool for detecting essential behaviors of animals (e.g., feeding, breathing, drinking, vocalization, and sensing) of various species (e.g., penguins: Wilson et al. 2002, Takahashi et al. 2004; pinnipeds: Liebsch et al. 2007; and sea turtles: Hochscheid et al. 2005, Myers & Hays 2006, Fossette et al. 2008, Houghton et al. 2008).

Dataloggers with accelerometer sensors have also provided novel insights into

the biology of animals (e.g., Yoda et al. 1999, Tanaka et al. 2001, Sato et al. 2003, and Wilson et al. 2006). For example, acceleration dataloggers provide the information on the angle and dynamic movements of the appendage (Tanaka et al. 2001), and enable to determine the classification of behavioral patterns and temporal characteristics of these patterns (Yoda et al. 2001, Wilson et al. 2008, Shepard et al. 2008). Acceleration dataloggers allow researchers to monitor the movements of isolated body parts of animals, as the IMASEN does. For example, its attachment to the head or lower mandible has enabled researchers to monitor the feeding events of seals (Naito 2007, Suzuki et al. *in press*). Previous studies have been conducted on the feeding and breathing behaviors of sea turtles using IMASENs (e.g., Hochscheid et al. 2005, Myers & Hays 2006, Fossette et al. 2008). Compared to the IMASEN, one of the benefits of the acceleration datalogger for determining feeding and breathing behaviors is that it can record head pitch as well as lower beak movements. The head pitch during feeding may provide additional information on feeding behavior, such as the situation or feeding location. In addition, based on the beak open-close motion detection by an IMASEN (Fossette et al. 2008), it is difficult to distinguish between feeding and breathing events, in which sea turtles open their mouths at the sea surface. When turtles breathe at the surface, they extend their neck upward (Reina et al. 2005). Therefore, if the breathing events were able to be distinguished the feeding event at the surface based on the analysis of the head pitch, this technique will be useful technique for studying the breathing behavior of sea turtles.

In the present study, we attached acceleration dataloggers to the lower beaks of loggerhead turtles (*Caretta caretta*) in a captive setting to assess the applicability of this monitoring technique for determining feeding and breathing behaviors in the wild. In addition, to examine beak movements associated with feeding, we provided different types of food to test whether the consumption of different kinds of food might result in different patterns of beak acceleration. The relationship between the head pitch of turtles and their feeding location in the water column was also examined.

MATERIALS AND METHODS

Experimental protocol and instruments

Our experiments were conducted in a 200 kiloliter tank (H x L x W= 10 m x 10 m x 2.2 m) at the Yaeyama station in the Stock Enhancement Technology Development Center, Seikai National Fisheries Research Institute, Fisheries Research Agency, Japan. Six captive juvenile loggerhead turtles were used to study feeding behavior, and one of these, Turtle B, was also used to study breathing movements (Table 1). All experiments were conducted, in accordance with the Japan Ethological Society guidelines for the experimental use of animals (http:// wwwsoc.nii.ac.jp/jes2/guideline.html).

An acceleration data logger (M190L-D2GT: 15-mm diameter, 53-mm length, 17 g in air, memory capacity of 8 million data points; Little Leonardo Co., Tokyo, Japan) was affixed to the lower beak of each loggerhead using epoxy putty (Konishi Co., Ltd. Osaka, Japan) and two-component epoxy resin (ITW Industry Co., Ltd. Osaka,

Japan) (Fig. 1). Acceleration dataloggers can record depth and temperature at 1-s intervals, and two-axis accelerations (surging and heaving) at 1/32-s intervals. Using these intervals, we can theoretically record data for about 70 hours. The maximum range of the depth sensor was up to 190 m, with a resolution of 0.046 m. The measurement range of the accelerometers was ± 39.2 m s^{-2}, with a resolution of 0.019 m s^{-2}.

Each turtle affixed with a datalogger was released into the tank and allowed to acclimate for more than one hour to recover from handling. The turtles were then fed squid rings (main bodies), fins, and heads (including arms and tentacles), and the times when the turtles bit prey were recorded by visual observation from above. The masses and lengths of the prey items are given in Table 3. For Turtle B, we also recorded the times when breaths were taken. After the experiments, the two-axis accelerations and depth data were downloaded from the recovered dataloggers. The temperature during the experiments ranged from 23 ^{o}C to 26 ^{o}C.

Extraction of breathing and feeding behaviors from acceleration data

High frequency acceleration signals represent animal movements such as flipper strokes and tail beats, which can be expressed by the component that remains after filtering out the low frequency signal from the original acceleration data (Tanaka et al. 2001, Yoda et al. 2001, Sato et al. 2003). Thus, we extracted the opening and closing motion of the lower beak from the surging and heaving acceleration data using, IGOR, IFDL

(WaveMatrics, Inc., USA) and Ethographer (S.Q. Sakamoto, Hokkaido University, for detail, see Sakamoto et al. 2009) software. In the present study, we defined a feeding signal as an acceleration greater than + 0.3 m s^{-2} or smaller than - 0.3 m s^{-2} in both the surging and heaving axes of lower beak motion, which was the most appropriate definition for a high detection rate and a low false detection rate, based on data analysis. In the case that two feeding signals were within 5 s of each other, they were regarded as one feeding event. To eliminate the noise pulse caused by contact with the tank wall and breathing behavior, we removed the feeding signals that occurred within 1 s of breathing or contact from the analysis. To determine whether the pitch of the head differs when feeding for prey on the bottom of tank versus the water column, we calculated the low frequency signals of the acceleration data, which are indicative of the pitch of the head during feeding (see below).

Sea turtles complete a single exhalation and inhalation with each respiration (Lutz & Bentley 1985, Kontos & Eckert 1988). When turtles breathe at the surface, they extend their neck upward (Reina et al. 2005). Therefore, the time spent breathing can be measured if the pitch of the head can be measured. The low frequency signals of the longitudinal accelerations allow estimation of the pitch of animals (body parts) tagged with a datalogger (Tanaka et al. 2001). In this study, we regarded the pitch of the lower beak as the pitch of the head, because the pitch of the lower beak is nearly equal to that of the head when turtles close their beaks. In addition, the open-close movements of the lower beak were represented by the high frequency signals. The pitch of the lower beak

175 was extracted by filtering out the high frequency signals from the surging acceleration
176 data with IGOR, IFDL (WaveMatrics, Inc., USA) and Ethographer (S.Q. Sakamoto,
177 Hokkaido University, in detail, see Sakamoto et al. 2009). Upward and downward
178 orientations were represented by positive and negative pitch values, respectively. We
179 defined breathing behavior as when the pitch was greater than 30^{o} and the water depth
180 was less than 0.15 m, which was the most appropriate definition to allow high detection
181 rate and low false detection rate, as demonstrated by data analysis.

182 Comparing the timing of feeding and breathing behaviors extracted from the
183 acceleration data with those from visual observation, we calculated the detection and
184 false detection rates of breathing and feeding behaviors. The detection rate was defined
185 as the ratio of the number of behaviors that were detected by both the acceleration data
186 and a visual observation to the number of the behaviors that were detected by visual
187 observation alone. The false detection rate was defined as the ratio of the number of
188 false detections of behaviors by acceleration data to the number of total behaviors
189 detected by acceleration data. Breathing and feeding behaviors extracted from
190 acceleration data were identified with those from visual observation if the time
191 difference between them was less than or equal to 3 s.

192

193 **Data analysis for feeding behavior**

194 To relate acceleration data characteristics during feeding behavior with specific prey
195 items, we looked at the relationships between the prey item mass and feeding duration

and the biting force. Biting force was calculated from the maximum value of the square sum of the high frequency components of the surging and heaving accelerations during feeding. Furthermore, for Turtles C through F, we investigated the relationship between the pitch of the head and the feeding location (bottom of tank versus water column), since we hypothesized that the turtles changed their head pitch depending on the feeding location after observing the experiments for Turtles A and B.

RESULTS

During the experiments, we fed six turtles 249 prey items in total, all of which were consumed. A feeding event was always initiated by a turtle holding a prey item while craning its neck forward and opening its beak widely. After this, the turtle would open and close its beak several times while holding on the prey item and then finally swallow it. During consumption, the lower beak wiggled not only up and down but also back and forth. This series of lower beak movements associated with feeding behavior was manifested as continuous feeding pulses in the acceleration data of both the surging and heaving axes (Fig. 2). The detection rates of feeding behaviors were nearly perfect (99.6 ± 1.1 %) for all six turtles, indicating that the feeding behavior of loggerhead turtles is successfully detected by the acceleration datalogger (Table 2). However, the mean false detection rate was 24.8 ± 12.4 %, indicating that the acceleration datalogger detected other movements of the lower beak or head that resembled feeding behavior based on the acceleration data but did not represent actual feeding.

There was no correlation between the biting force and feeding duration (Spearman rank correlation test, $r_s = 0.18$, N = 205, $P > 0.05$), although the bite force during feeding was significantly different between types of prey (Kruskal-Wallis test, H = 15.3, df = 2, $P < 0.01$). The biting force associated with feeding the rings of the main body differed significantly from that involved in feeding the head (*post-hoc* Scheffe test, $P < 0.01$; Table 3). The length and mass of the prey items did not correlate with the bite force (Spearman rank correlation test, $r_s = 0.03$, N = 181, $P > 0.05$ for length; $r_s = 0.09$, N = 205, $P > 0.05$ for mass). There was no difference in feeding duration between the types of prey (Kruskal-Wallis test, H = 4.21, df = 2, $P > 0.05$), nor was there a correlation between feeding duration and length or mass of the prey (Spearman rank correlation test, $r_s = 0.05$, N = 181, $P > 0.05$ for length; $r_s = 0.01$, N = 205, $P > 0.05$ for mass). The turtles positioned their necks slightly downward (- 16 ± 17 ^{o}) when feeding on the bottom of the tank, whereas in the water column, they approached the prey with their heads in a nearly horizontal position (2 ± 11 ^{o}). These positions were significantly different (Man-Whitney test, Z = 6.30, $P < 0.0001$).

Forty breathing events were observed for Turtle B during the experiment. Our observations reveal that respiration was always done with the neck arched upward. From the pitch and depth data, we could infer that the turtle swam up to the surface to breathe and then extended its neck upward (Fig. 3). All breathing events (n = 40) were detected by the datalogger, and the false detection rate was only 2.4 percent (1/ 41). The mean duration of the detected breathing events was 1.99 ± 0.56 seconds.

Specific movements of the lower beak were not observed except during feeding and breathing, although we did observe that the turtles bit and held onto the polyvinyl chloride (PVC) pipes and outshoots in the tank. The buccal oscillations reported by previous studies (Hochscheid et al. 2005, Myers & Hays 2006, Houghton et al. 2008) were not detectable by analyzing the acceleration data profiles of the lower beak.

DISCUSSION

Our results demonstrate that the acceleration dataloggers were able to detect the lower beak movements of loggerhead turtles. The acceleration data enabled us to identify both feeding and breathing behaviors. Because the acceleration datalogger in this study is a single-packaged device of a sensor and logger, it does not need sensor cables. Therefore, it is easy to attach to the lower beak of turtle and is free from the device problems and influences on the behavior of animals that are caused by sensor cables (e.g., Wilson et al. 2002). Therefore, the acceleration datalogger could be an alternative tool for studying feeding ecology and diving physiology in sea turtles.

The nearly perfect detection rate of feeding behavior attained in this study indicates that this method for detection is highly sensitive. In the present study, the false detection rate was about 25 %, although this value would likely change under field conditions. We observed that the turtles sometimes bit and held the PVC pipes and outshoots in the tank. Therefore, a possible reason for false detection is the detection of the movements of the head or lower beak similar to those in feeding. This result

indicates that the detection of feeding behavior by the acceleration datalogger might also indicate other similar behaviors. However, this technique for the detection of feeding behavior could provide an index of feeding effort similar to the technique using the IMASEN (Fossette et al. 2008), which would offer new insights into the feeding ecology of sea turtles.

From the acceleration datalogger, we were able to infer the feeding duration, biting force and head pitch. The biting force was greater when eating the intricately-shaped heads of squid, including the arms and tentacles, than when feeding the ring of the main body (Table 3). When the IMASEN is used in field studies, the degree of the inter-mandibular distance is not investigated because the Hall signal is highly affected by water pressure in relation to depth (Fossette et al. 2008). Such mechanical problems in relation to water pressure have not yet been reported for the acceleration datalogger. Thus, the acceleration datalogger has the advantage of being able to detect the degree of biting force of sea turtles during feeding. Additionally, the pitch of the head was slightly downward when feeding on the bottom of the tank, but it was close to horizontal when feeding in the water column. These results indicate that the data from an acceleration datalogger accurately represent the movements and posture of turtle heads. However, the kinds of prey preferred by sea turtles differ between species, populations and life stages of sea turtles (Mortimer 1995, Bjorndal 1997). In the present study, we could not simulate all of the possible prey items of loggerhead turtles in the wild to evaluate the possibility of their detection by the

acceleration datalogger in the field. Still, the open-close movements of the lower beak are considered to be common to feeding for all of the different prey of loggerheads. Therefore, our results demonstrate that it is possible to determine whether feeding on the prey requires a strong biting force, and to differentiate between feeding on the sea floor and feeding in the water column.

We also detected the breathing behavior of a loggerhead turtle from its head pitch, which suggests acceleration dataloggers may be useful for measuring the respiratory frequency of loggerheads. The breathing behavior of Turtle B was comprehensively detected, and we were able to distinguish it completely from feeding behavior at the surface, which is a concern when using the IMASEN (Fossette et al. 2008). The false detection rate was very low. False detection occurred when the turtle swam up to the surface just before breathing. Usually, before arriving at the surface, the pitch of the turtle's neck was less than 30 ^{o}, and then increased to greater than 30 ^{o} during breathing (Fig. 2). The cause of the false detection was steep ascent to the surface at an angle greater than 30 ^{o}. The breathing duration was also calculated in the present study. The approximately 2 second breathing duration in the present study is very similar to that recorded for juvenile loggerhead turtles by using the IMASEN (2-3 seconds; Hochscheid et al. 2005), and adult female leatherback turtles (*Dermochelys coriacea*) (about 3 seconds; Reina et al. 2005). The breathing duration calculated in the present study may represent the period in which turtles complete a single respiration. However, further study will be needed to investigate the relationship between the

301 breathing duration calculated by acceleration and depth data, and tidal volume.

302 Buccal oscillations of sea turtles, which might represent the state of
303 consciousness of turtles (Houghton et al. 2008) and their sensing of the immediate
304 environment (Hochscheid et al. 2005, Myers & Hays 2006), were not detectable by
305 using the acceleration dataloggers, which is a disadvantage compared to the IMASEN.
306 Therefore, this detection technique for the lower beak movements may be an inadequate
307 tool for studies on the buccal oscillations of sea turtles.

308 In conclusion, the attachment of acceleration dataloggers to the lower beaks of
309 loggerheads allows monitoring of the feeding and breathing behaviors of sea turtles.
310 Future field studies using this device may provide additional information on the biology
311 of sea turtles, including more precise classifications of their behavioral patterns, such as
312 feeding and breathing, and the temporal distribution of these behaviors. This will be
313 possible because acceleration dataloggers provide information on an animal's posture,
314 dynamic movements and activity level (e.g., Wilson et al. 2006, Halsey et al. 2008). By
315 attaching acceleration dataloggers to the lower beak and body of diving animals, novel
316 insights could be gained into the diving physiology of free-living animals, such as the
317 relationships between dive duration, respiratory behavior, and the amount of activity.

318

319 **ACKNOWLEDGEMENTS**

320 We would like to acknowledge Dr. K. Okuzawa (Ishigaki Tropical Station, Seikai
321 National Fisheries Research Institute) for his kind assistance with experiments. We also

thank the staffs of the Ishigaki Tropical Station and Yaeyama station, Seikai National Fisheries Research Institute for research help and constructive comments. We are grateful for the experimental assistance of Dr. N. Naito. This study was supported by the GCOE program "Informatics Education and Research Center for Knowledge-Circulating Society".

REFERENCES

Bjorndal KA (1997) Feeding ecology and nutrition of sea turtles. In: Lutz PL, Musick JA (eds) The Biology of Sea Turtles. CRC Press, Boca Raton p 199-231

Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Wolcott TG, Butler PJ (2004) Biotelemetry: a mechanistic approach to ecology. Trends Ecol Evol 19: 334-343

Fossette S, Gasper P, Handrich Y, Maho YL, Georges JY (2008) Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during interesting intervals in French Guiana. J Anim Ecol 77: 236-246

Halsey LG, Shepard ELC, Hulston CJ, Jeukendrup AE, Venables MC, White CR, Wilson RP (2008) Acceleration versus heart rate for assessing energy expenditure during locomotion in free-living animals: the effect of gait and incline in humans. Zoology 111: 231-241

Hawkins P (2004) Bio-logging and animal welfare: practical refinements. Mem Natl Inst Polar Res Spec Issue 58: 58-68

Hays GC, Metcalfe JD, Walne AW, Wilson RP (2004) First records of flipper beat frequency during sea turtle diving. J Exp Mar Biol Ecol 303: 243-260

Hochscheid S, Maffuccia F, Bentivegna F, Wilson RP (2005) Gulps, wheezes, and sniffs: how measurement of beak movement in sea turtles can elucidate their behaviour and ecology. J Exp Mar Biol Ecol 316: 45-53

Houghton JDR, Cedras A, Myers AE, Liebsch N, Metcalfe JD, Mortimer JA, Hays GC (2008) Measuring the state of consciousness in a free-living diving sea turtle. J Exp Mar Biol Ecol 356: 115-120

Kontos A, Eckert SA (1988) The relationship between the number of breaths, surface time and dive time of the hawksbill turtle (*Eretmochelys imbricata*) in the wild. Am Zool 28: 180A

Liebsch N, Wilson RP, Bornemann H, Adelung D, Plotz J (2007) Mouthing off about fish capture: Jaw movement in pinnipeds reveals the real secrets of ingestion. Deep Sea

364 Res Part II 54:256-269

365

366 Lutz PL, Bentley PJ (1985) Respiratory physiology of diving in the sea turtle. Copeia
367 1985: 671-679

368

369 Mortimer JA (1995) Feeding ecology of sea turtles. In: Bjorndal KA (ed) Biology and
370 Conservation of Sea Turtles. Smithsonian Institution Press, Washinton, p 103-109

371

372 Myers AE, Hays GC (2006) Do leatherback turtles (*Dermochelys coriacea*) forage
373 during the breeding season? A combination of novel and traditional data logging devices
374 provide new insight. Mar Ecol Prog Ser 322: 259-267

375

376 Naito Y (2004) Bio-logging science. Mem Natl Inst Polar Res Spec Issue 58: 118-32

377

378 Naito Y (2007) How can we observe the underwater feeding behavior of endotherms.
379 Polar Sci 1: 101-111

380

381 Reina RD, Abernathy LJ, Marshall GJ, Spotila JR (2005) Respiratory frequency, dive
382 behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during
383 the inter-nesting interval. J Exp Mar Biol Ecol 316: 1-16

384

385 Ropert-Coudert Y, Wilson RP (2005) Trends and perspectives in animal-attached remote
386 sensing. Front Ecol Environ 3(8): 437-444
387
388 Sakamoto SQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S
389 (2009) Can Ethograms Be Automatically Generated Using Body Acceleration Data
390 from Free-Ranging Birds? PLoS ONE 4(4) e5379, doi; 10.1371/journal.pone.0005379
391
392 Sato K, Mitani Y, Cameron F, Siniff BD, Naito Y (2003) Factors affecting stroking
393 patterns and body angle in diving Weddell seals under natural conditions. J Exp Biol
394 206: 1461-1470
395
396 Shepard ELC, Wilson RP, Liebsch N, Quintana F, Gomez Laich A, Lucke K (2008)
397 Flexible paddle sheds new light on speed; a novel method for the remote measurement
398 of speed in aquatic animals. Endang Species Res (*in press*)
399
400 Suzuki I, Naito Y, Folkow LP, Miyazaki N, Blix AS (2009) Validation of a device for
401 accurate timing of feeding events in marine animals. Polar Biol (*in press*)
402
403 Takahashi A, Dunn MJ, Trathan PN, Croxall JP, Wilson RP, Sato K, Naito Y (2004)
404 Krill-feeding behavior in a chinstrap penguin *Pygoscelis antarctica* compared with
405 fish-eating in magellanic penguins *Speniscus magellanicus*: a pilot study. Mar Ornithol

406 32: 47-54

407

408 Tanaka H, Takagi Y, Naito Y (2001) Swimming speeds and buoyancy compensation of
409 migrating adult chum salmon *Oncorhynchus keta* revealed by speed/ depth/ acceleration
410 data logger. J Exp Biol 204: 3895-3904

411

412 Yoda K, Naito Y, Sato K, Takahashi A, Nishikawa J, Ropert-coudert Y, Kurita M, Le
413 Maho Y (2001) A new technique for monitoring the behavior of free-ranging Adélie
414 penguins. J Exp Biol 204: 685-690

415

416 Yoda K, Sato K, Niizuma Y, Kurita M, Bost CA, Le Maho Y, Naito Y (1999) Precise
417 monitoring of porpoising behaviour of Adelie penguins determined using acceleration
418 data loggers. J Exp Biol 202: 3121-3126

419

420 Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal
421 lives: use of a daily diary on animals. Endang Species Res 4: 123-137

422

423 Wilson RP, Steinfurth A, Ropert-Coudert Y, Kato A, Kurita M (2002) Lip-reading in
424 remote subjects: an attempt to quantify and separate ingestion, breathing and
425 vocalisation in free-living animals using penguins as a model. Mar Biol 140: 17-27

426

427 Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006)
428 Moving towards acceleration for estimates of activity-specific metabolic rate in
429 free-living animals: the case of the cormorant. J Anim Ecol 75: 1081-1090

430

431

Table 1 *Caretta caretta*. Physical characteristics of experimental turtles and summary of experiments

ID	SCL (cm)	BW (kg)	Monitoring item	Total observation period (min.)	Date of experiment
Turtle A	57.2	34.2	Feeding	66	19-20/04/2008
Turtle B	63.3	35.4	Feeding + Respiratory	72	22-23/04/2008
Turtle C	60.5	36.0	Feeding	95	10-12/05/2008
Turtle D	62.0	38.9	Feeding	67	12-13/05/2008
Turtle E	64.7	36.0	Feeding	88	13-15/05/2008
Turtle F	61.6	36.0	Feeding	74	15-16/05/2008

Table 2 *Caretta caretta*. Detection and false detection rates of feeding behavior by the acceleration datalogger

ID	Detection rate of feeding (%)	False detection rate of feeding (%)
Turtle A	97.4 (38/39)	13.6 (6/44)
Turtle B	100.0 (29/29)	9.4 (3/32)
Turtle C	100.0 (72/72)	16.3 (14/86)
Turtle D	100.0 (24/24)	35.1 (13/37)
Turtle E	100.0 (47/47)	32.9 (23/70)
Turtle F	100.0 (38/38)	37.7 (23/61)
	99.6 ± 1.1 (248/249)	24.8 ± 12.4 (82/330)

Table 3 Lengths and masses of food items provided during the experiments

	Length (cm)	Mass (g)	Biting force (m/s^2)	Feeding duration (s)
Rings of main body (n=142)	2.8 ± 0.8	19.4 ± 5.4	8.7 ± 4.1 *	10.6 ± 9.2
Fins (n=39)	5.1 ± 1.8	11.5 ± 4.6	10.4 ± 5.2	10.4 ± 5.1
Heads (n=24)	-	30.3 ± 5.7	11.5 ± 3.7 *	11.3 ± 5.5

439 Asterisks represent significant differences between marked groups

440

441 Figure legend

442 Fig.1 *Caretta caretta*. Schematic drawing of attachment site of acceleration datalogger
443 on the lower beak of a loggerhead turtle. Attachment was accomplished using epoxy
444 putty (See the text for details).

445

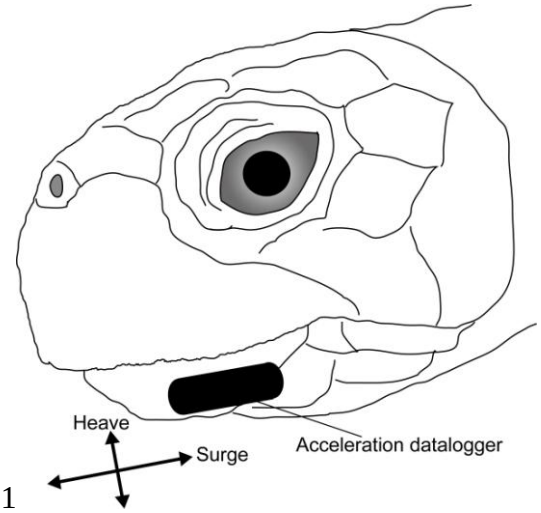
446 Fig.2 *Caretta caretta.* A typical profile of feeding behavior, showing heaving and
447 surging accelerations of the lower beak, and depth. Horizontal broken lines in heaving
448 and surging acceleration profiles represent the thresholds for indentifying feeding pulse
449 (See the text for details). Horizontal bars on the bottom represent the time the turtle
450 holds food items into their mouth (identified by visual observation), the time the feeding
451 pulses occur, and feeding duration.

452

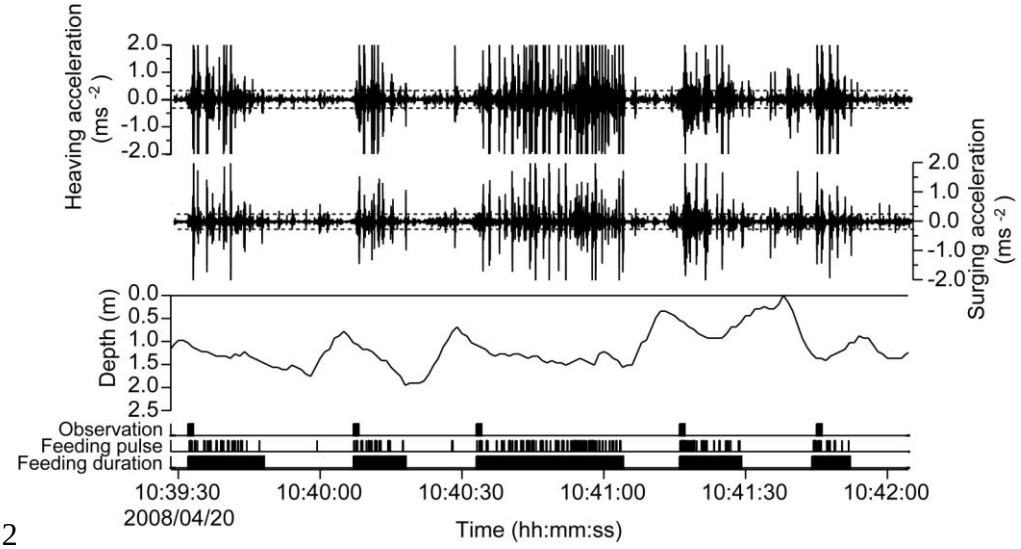
453 Fig.3 *Caretta caretta.* A typical profile of breathing behavior, showing heaving
454 acceleration of the lower beak, head pitch, and depth. Horizontal broken lines in head
455 pitch and depth profiles represent the thresholds for indentifying breathing behavior
456 (See the text for details). Horizontal bars on the bottom represent breathing duration.

457

458

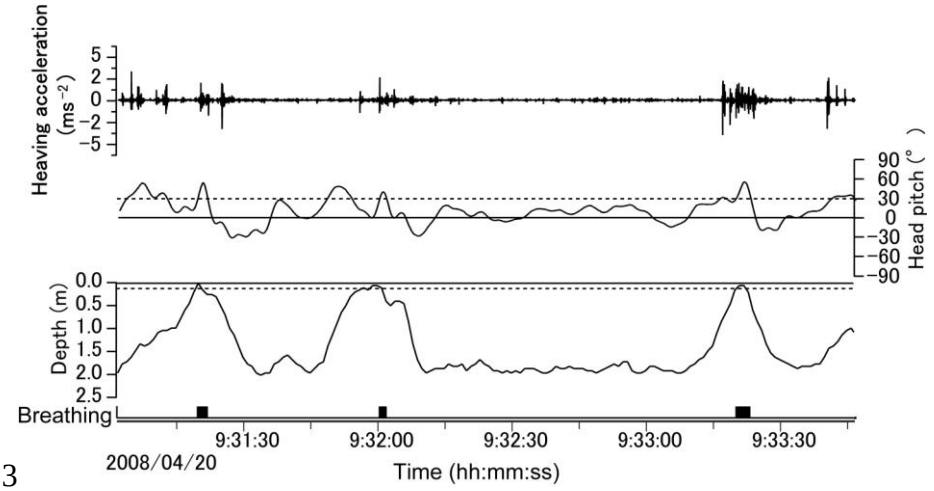


459 Fig.1



460 Fig.2

461



462 Fig.3